

The voice from the hereafter: vocalisations in three species of *Atelopus* from the Venezuelan Andes, likely to be extinct

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Abstract

Atelopus is a species-rich group of Neotropical bufonids. Present knowledge on bioacoustics in this genus is relatively poor, as vocalisations have been described in only about one fifth of the ca. 100 species known. All studied members of the genus produce vocalisations although, with a few exceptions, most species lack a middle ear. Nonetheless, hearing has been demonstrated even in earless *Atelopus* making bioacoustics in these toads an inspiring research field. So far, three structural call types have been identified in the genus. As sympatry is uncommon in *Atelopus*, calls of the same type often vary little between species. Based on recordings from the 1980s, we describe vocalisations of three Venezuelan species (*A. carbonerensis*, *A. mucubajensis*, *A. tamaense*) from the Cordillera de Mérida, commonly known as the Andes of Venezuela and the Tamá Massif, a Venezuelan spur of the Colombian Cordillera Oriental. Vocalisations correspond, in part, to the previously identified call types in *Atelopus*. Evaluation of the vocalisations of the three species presented in this study leads us to recognise a fourth structural call type for the genus. With this new addition, the *Atelopus* acoustic repertoire now includes (1) pulsed calls, (2) pure tone calls, (3) pulsed short calls and (4) pure tone short calls. The call descriptions provided here are valuable contributions to the bioacoustics of these Venezuelan *Atelopus* species, since all of them have experienced dramatic population declines that limit possibilities of further studies.

Key Words

Anura, Bufonidae, *Atelopus carbonerensis*, *Atelopus mucubajensis*, *Atelopus tamaense*, bioacoustics

Introduction

Atelopus Duméril & Bibron, 1841, is a monophyletic lineage of Neotropical bufonids of Cretaceous origin (Pramuk et al. 2008; Lötters et al. 2011). More than 100 species are currently recognised, with several of them remaining

undescribed and most of them living in the Andean mountain ranges (La Marca et al. 2005; Rueda-Almonacid et al. 2005). From the Cordillera de Mérida, Venezuela and the Tamá Massif, a Venezuelan spur of the Cordillera Oriental

of Colombia, seven species of *Atelopus*, inhabiting cloud forests and páramos, are known: *A. carbonerensis* Rivero, 1974; *A. chrysocorallus* La Marca, 1996; *A. mucubajiensis* Rivero 1974; *A. pinangoi* Rivero, 1982; *A. soriano* La Marca, 1983; *A. tamaense* La Marca, García-Pérez & Renjifo, 1990; and another still undescribed species (La Marca and Lötters 1997; Rueda-Almonacid et al. 2005).

Over the last four decades, along with most species of the genus (see overview in La Marca and Lötters 2008), the *Atelopus* species from the Cordillera de Mérida have dramatically declined. The same is expected for *A. tamaense*, although its only known site has apparently never been revisited since the species' discovery (La Marca and Reinthaler 1991; La Marca 1995; 2004; La Marca et al. 2005; Young et al. 2001; Lötters et al. 2005; Rueda-Almonacid et al. 2005). All these species are considered as Critically Endangered with decreasing population trends under the IUCN Red List of Threatened Species (IUCN 2019). Various reasons have been discussed for this decrease, such as chytridiomycosis, an emerging infectious disease caused by the amphibian skin fungus *Batrachochytrium dendrobatidis* which is of Asian origin (O'Hanlon et al. 2018), to likely play a key role (La Marca and Lötters 1997; La Marca et al. 2005; Lampo et al. 2006). Despite increased search and monitoring efforts, only a single individual of *A. mucubajiensis* was found in 2004 (Lampo et al. 2006). Prior to this, the last *Atelopus* specimen seen was one of *A. carbonerensis* in 1998 (Stuart et al. 2008). We consider that most, if not all, populations of the *Atelopus* species from the Cordillera de Mérida and the Tamá Massif are likely already extinct.

All *Atelopus* species lack a tympanum and most lack a columella (McDiarmid 1971; Lötters 1996). As a consequence, it has been suggested that, throughout the genus, vocalisations have undergone only a 'conservative' evolution. It has been hypothesised that this is a result of the widespread lack of sympatry of two or more species of the genus (e.g. Cocroft et al. 1990; Lötters 1996). In addition, all *Atelopus* species are associated with streams and this often noisy environment is assumed to exert similar selective pressures on the communication system of species (Cocroft et al. 1990). In line with this, visual communication (e.g. forelimb waving), has also been reported to occur in some species (Lindquist and Hetherington 1996; Lötters et al. 2002a). However, distinct structural call types have been identified in several *Atelopus* species, related to various intra- and interspecific interactions, although poorly studied (see below). This suggests that calling may indeed play a role in the genus, perhaps in a multimodal signalling context, as known from other stream-dwelling anurans (Preininger et al. 2013). Moreover, hearing has in fact been demonstrated in *A. chiri-quiensis* and *A. franciscus* (Jaslow and Lombard 1996; Boistel et al. 2011). These observations indicate that vocalisation in *Atelopus* is still an inspiring research field.

Bioacoustics in the seven members of the genus from the Cordillera de Mérida and Tamá Massif are still unstudied. Back in the 1980s, two of the authors (DM and

ELM) recorded calls of *A. carbonerensis*, *A. mucubajiensis* and *A. tamaense* (Fig. 1). In the present paper, we describe vocalisations in these species for the first time and discuss the acoustic communication system of the genus.

Atelopus vocalisations

As a milestone in bioacoustics of the genus, Cocroft et al. (1990) reviewed *Atelopus* vocalisations and defined three call types, emitted by males. They differ in structure and duration (this is why the term 'call type' is not meant in a functional way as in common literature; e.g. Köhler et al. 2017) and each are quite similar across the various species: (1) pulsed calls having a duration of 227–1240 ms; (2) pure tone calls lasting 180–297 ms; (3) short calls that are pulsed or unpulsed with a duration of 22–100 ms. Following the definition and terminology of Köhler et al. (2017), pure tone calls might actually be referred to as 'tonal calls'. However, for reasons of comparability with previous *Atelopus* call descriptions, we refrain from a name change.

All three call types may occur in a single species of *Atelopus* (Table 1). The authors also reported 'other calls', which perhaps may best be interpreted as partial or intermediate calls (Cocroft et al. 1990; Lötters et al. 2002a). As only a few behavioural studies in *Atelopus* exist, the functionality of the different calls has, therefore, been rather interpreted, corresponding to the function of similar calls in other bufonids (cf. Martin 1972; Wells 2007). Thus, pulsed and short calls are regarded as advertisement and release calls, respectively (e.g. Cocroft et al. 1990; Lindquist and Hetherington 1996).

In addition to the 13 taxa in which vocalisations were known by the time of Cocroft et al. (1990), vocalisations in seven other *Atelopus* species have been described (Table 1). Calls in these species can be classified according to the three structural call types mentioned. However, additional data demonstrate a higher variation in call duration than proposed by Cocroft et al. (1990): pulsed calls can be shorter (92–108 ms in *A. tricolor*, Lötters et al. 1999; 110–130 ms in *A. pulcher*, Lötters et al. 2002b; 205–295 ms in *A. limosus*, Ibáñez et al. 1995), pure tone calls can be longer (290–420 ms in *A. reticulatus*, Lötters et al. 2002a), short calls can be both shorter (5–16 ms in *A. limosus*, Ibáñez et al. 1995) and longer (44–114 ms in *A. peruensis*, Lötters et al. 1999; mean 135 ms in *A. nahumae*, Ortega et al. 2017).

Since only anecdotal descriptions of vocalisations from other *Atelopus* species exist (e.g. on *A. arthuri* and *A. ignescens* by Peters 1973), our knowledge on bioacoustics in this genus is based on only about one fifth of all species known so far. Moreover, at least in *A. laetissimus*, it has been suggested that females can also emit calls (Rocha Usuga et al. 2017) which requires further studies. Amongst the Venezuelan *Atelopus* species, merely vocalisations of *A. cruciger* from the Cordillera de la Costa have been described (Cocroft et al. 1990).

Table 1. Reported structural call types in the genus *Atelopus*, an update and refinement of Cocroft et al. (1990: 640), who only distinguished pulsed calls, pure tone calls and short calls. Species, in which ‘other calls’ (see text) are known, are marked with an asterisk. Applied taxonomy, if different to original call description, is based on Noonan and Gaucher (2005) for *A. barbotini*, Lötters et al. (2002b) for *A. hoogmoedi*, Richards and Knowles (2007) for *A. varius*, unpubl. data (SL) for *A. sp.* ‘Itaya’ and De la Riva et al. (2011) for *A. cf. loettersi*.

Species	Pulsed call	Pure tone call	Short pulsed Call	Short pure tone call	Source(s)
<i>A. barbotini</i>	×				Lescure 1981 (as <i>A. spumarius barbotini</i>)
<i>A. carbonerensis</i> *	×	×	×	×	This paper
<i>A. chiriquiensis</i>	×	×	×		Jaslow 1979; Lötters et al. 1999
<i>A. cruciger</i> *	×	×	×		Cocroft et al. 1990
<i>A. exiguus</i>	×				Coloma et al. 2000
<i>A. flavescens</i>	×				Lescure 1981
<i>A. franciscus</i>	×				Lescure 1981; Boistel et al. 2011
<i>A. hoogmoedi</i>	×				Lescure 1981; Cocroft et al. 1990 (as <i>A. spumarius hoogmoedi</i>)
<i>A. limosus</i>	×		×		Ibáñez et al. 1995
<i>A. minutulus</i> *	×	×	×		Cocroft et al. 1990
<i>A. mucubajiensis</i>		×		×	This paper
<i>A. nahumae</i>				×	Ortega et al. 2017
<i>A. nicefori</i>	×				Cocroft et al. 1990
<i>A. pulcher</i>	×		×		Lötters et al. 2002b
<i>A. peruensis</i>			×		Lötters et al. 1999
<i>A. reticulatus</i>		×			Lötters et al. 2002a
<i>A. senex</i>	×				Cocroft et al. 1990
<i>A. tamaense</i>				×	This paper
<i>A. tricolor</i>	×		×		Lötters et al. 1999
<i>A. varius</i>	×		×	×	Starrett 1967; Cocroft et al. 1990 (in part as <i>A. zeteki</i>)
<i>Atelopus</i> sp. ‘Panama’			×		Cocroft et al. 1990 (cf. <i>A. limosus</i>)
<i>Atelopus</i> sp. ‘Itaya’	×				Asquith and Altig 1987 (as <i>A. spumarius</i>)
<i>Atelopus</i> cf. <i>loettersi</i>			×		Cocroft et al. 1990 (as <i>A. s. spumarius</i>)



Figure 1. Three likely extinct species of *Atelopus* from Venezuela studied in this paper, from left to right, *A. carbonerensis* (out of SMNS series mentioned in text), *A. mucubajiensis* (specimen not collected), *A. tamaense* (ULABG 1820, holotype). Photographs by DM, ELM and Juan Manuel Renjifo.

Materials and methods

Details of recordings are provided in Table 2. For those of *A. carbonerensis*, a Sony TC 55 tape recorder with integrated microphone was used by DM. Voucher specimens were deposited at the Staatliches Museum für Naturkunde, Stuttgart (SMNS 11941, 4 specimens; SMNS 12625, 6 specimens), SVL 31–33 mm (6 males), 36–40 mm (4 females, that did not produce sounds). Recordings by ELM were made with a hand-held magnetic tape recorder (Sony TCS 310). The voucher specimens (all males) were deposited at the Universidad de Los Andes, Laboratorio de Biogeografía, Collection of Amphibians and Reptiles, Mérida (*A. carbonerensis*, ULABG 1706, SVL 44.0 mm; *A. mucu-*

bajiensis, SVL 34.5 mm, ULABG 2638; *A. tamaense*, ULABG 1820, SVL 37.0 mm). Recordings were digitised using the analogue-digital converters of a Digidesign Pro-Tools HD Accel system (Avid, Burlington/MA, USA) with a sampling rate of 44 kHz and 24-bit resolution and were saved as uncompressed *.wav files. All original recordings are provided as Suppl. materials to this paper.

Calls were analysed using the software Raven pro 1.5 Beta version (44.1 kHz sample rate, 16-bit) (Bioacoustics Research Program 2014). Frequency information was generated through Fast Fourier Transformation (FFT, width 2,048 samples). Spectrograms were obtained using the Blackman window function at 3db Filter Bandwidth of 512 Hz; overlap 90%. The spectral structure posterior to a note

Table 2. Details of *Atelopus* call recordings studied in this paper. An asterisk means that one or more vouchers are available (see Materials and methods). For additional information see figure legends.

Species	Site	Date, recorded by	Remark(s)
<i>A. carbonerensis</i>	La Carbonera, San Eusebio Forest (2,400 m a.s.l., Mérida State)	25 May 1986 by ELM*	During daytime (~10 am), distance to recorder ca. 0.3 and ca. 0.7 m (two recordings)
<i>A. carbonerensis</i>	La Carbonera, San Eusebio (2,330 m a.s.l., Mérida State)	10 June 1987 by DM*	Shortly before noon, distance to recorder ca. 1.5 m
<i>A. mucubajiensis</i>	Páramo La Corcovada, cerca Laguna La Victoria (3,000 m a.s.l., Mérida State)	23 June 1982 by ELM	During daytime (4:40 pm), distance to recorder ca. 0.3 m
<i>A. mucubajiensis</i>	La Corcovada, ca. Laguna Mucubaji (3,050 m a.s.l., Mérida State)	7 June 1989 by ELM*	During daytime (12:45 am), distance to recorder ca. 2 m
<i>A. tamaense</i>	Páramo de Tamá (2,950 m a.s.l., Apure State)	12 August 1987 by ELM*	During daytime, distance to recorder < 2 m

was not considered in the analyses to avoid echo effects. The end of a call was defined by a threshold of 0.015 s of silence.

Temporal measurements of calls such as repetition rates, duration of notes and number of pulses, were taken on the waveforms. Terminology of call descriptions follows Köhler et al. (2017). Regarding the terms advertisement, aggressive and release calls, we follow the definitions of Wells (2007).

Results and discussion

Atelopus carbonerensis

We recorded a series of typical pulsed calls from a male (Fig. 2, Table 3). In measurements, structure and energy distribution, they highly resemble those of other species of the genus (Cocroft et al. 1990), i.e. having the maximum frequency and amplitude rising gradually and reaching a climax shortly before the end. The first pulse is about two times longer than the remaining ones. The recording was taken from a male in amplexus with a conspecific female during the reproduction period in May 1986. Various other, partly non-amplectant males were emitting the same call type, which can be heard on the original tape. Along with previous authors describing *Atelopus* pulsed calls (e.g. Cocroft et al. 1990), we conclude that pulsed calls in *A. carbonerensis* can be considered male advertisement calls as per the definition of Wells (2007). According to this author, the main functions of these calls are defence of territory, maintenance of space amongst males and attraction of females. Once in amplexus, *A. carbonerensis* apparently can continue emitting advertisement calls, which has also been observed in other *Atelopus* species (SL unpubl. data). As these anurans aggregate for reproduction, this behaviour may well be linked to the maintenance of space.

We further recorded typical short calls from the same specimen (Fig. 3, Table 3) that are pulsed (with the last pulse about four times longer than the others) and frequency-modulated. In structure and energy distribution, they clearly resemble short calls of most other *Atelopus* species (Cocroft et al. 1990; Lötters et al. 1999). However, the present data from *A. carbonerensis* suggest that short calls can exceed the known maximum duration known in the genus so far (i.e. 108 ms in *A. peruensis*, see above). As

a consequence, *Atelopus* short calls may be redefined as ranging from 5–171 ms, with *A. limosus* (see above) and *A. carbonerensis* (Table 3) as the extremes. We have no doubt about the release function of short calls in *A. carbonerensis* (like in other congeners, see above), as these vocalisations were emitted by the amplectant male when other males (or the human collector) tried to physically interact.

In another interaction in which multiple males were involved (and in physical contact) during mating in June 1987, pure tone calls were recorded (Figs 4, 5, Table 3).

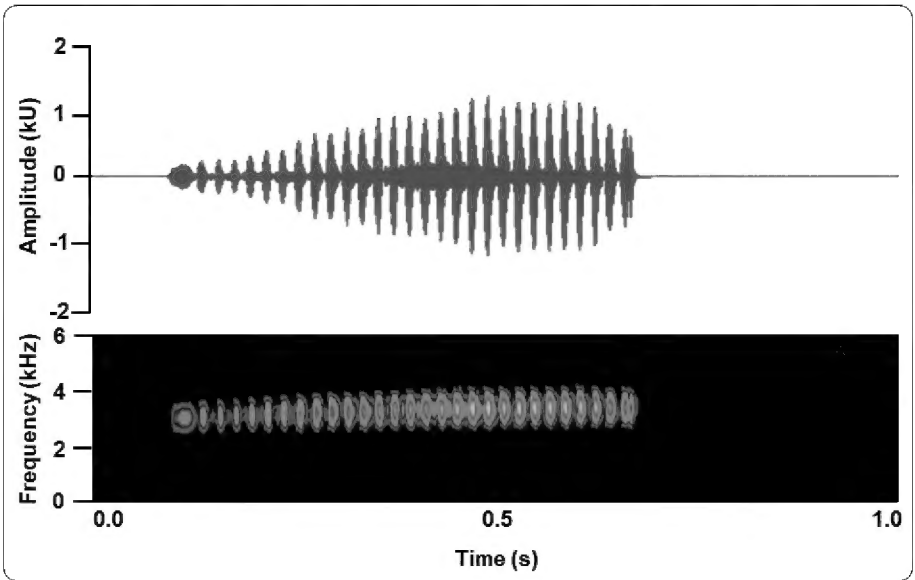


Figure 2. Oscillogram and spectrogram of a pulsed call of *A. carbonerensis* (ULABG 1706), recorded 25 May 1986 at Eusebio Forest (2,400 m a.s.l.), La Carbonera, Mérida State; distance to recorder ca. 0.7 m; 17.5 °C air temperature.

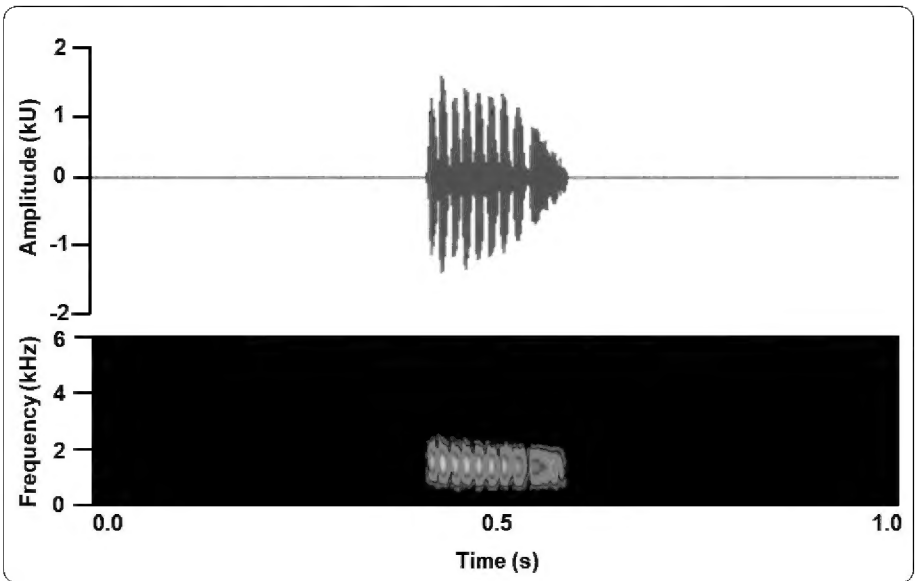


Figure 3. Oscillogram and spectrogram of a pulsed short call of *A. carbonerensis* (ULABG 1706), recorded 25 May 1986 at Eusebio Forest (2,400 m a.s.l.), La Carbonera, Mérida State; distance to recorder ca. 0.3 m; 17.5 °C air temperature.

Table 3. Characteristics of vocalisations in three Venezuelan *Atelopus* species. The mean is followed by the standard deviation and the range in parentheses. Frequency is abbreviated frequ. Pulsed, pure tone, pulsed short and pure tone short calls are as defined in the text.

Species Calls analysed Figure reference	Call type	Call duration (ms)	Interval between calls (ms)	Pulse rate/sec	Pulse length (ms)	Lower frequ. range (Hz)	Higher frequ. range (Hz)	Dominant frequ. (Hz)	Amplitude (KU)
<i>A. carbonerensis</i> N = 6 Fig. 2	Pulsed	575 ± 38 (478–623)	3601 ± 994 (1473–5389)	0.48	14 ± 4 (4–32)	2580 ± 110 (2380–2770)	4020 ± 62 (3920–4100)	3410 ± 21 (3380–3450)	1.10 ± 0.504 (0.37–1.87)
<i>A. carbonerensis</i> N = 8 Fig. 3	Pulsed short	136 ± 25 (74–171)	5181 ± 4172 (1041–13870)	0.11	14 ± 1 (7–48)	680 ± 81 (580–840)	2110 ± 98 (1910–2260)	1430 ± 44 (1380–1500)	13.94 ± 7.319 (6.45–32.76)
<i>A. carbonerensis</i> N = 11 Fig. 4	Pure tone	273 ± 59 (202–347)	3732 ± 2860 (872–6591)	n/a	n/a	890 ± 37 (850–940)	2000 ± 118 (1880–2160)	1390 ± 37 (1360–1440)	3.60 ± 0.679 (3.17–4.53)
<i>A. carbonerensis</i> N = 13 Fig. 5	Pure tone short	21 ± 10 (8–47)	3059 ± 2884 (140–9379)	n/a	n/a	730 ± 99 (600–1050)	1840 ± 206 (1540–2260)	1330 ± 151 (1160–1810)	6.20 ± 3.848 (2.43–18.29)
<i>A. mucubajiensis</i> N = 8 Fig. 6	Pure tone	243 ± 48 (159–337)	3704 ± 59 (3179–45605)	n/a	n/a	1760 ± 138 (1550–2040)	3170 ± 836 (2710–5350)	2420 ± 763 (2340–2580)	0.22 ± 0.255 (0.09–0.90)
<i>A. mucubajiensis</i> N = 17 Fig. 7	Pure tone short	41 ± 10 (22–57)	2122 ± 2059 (50–8395)	n/a	n/a	1030 ± 110 (860–1310)	2240 ± 183 (1960–2460)	1620 ± 1101 (2540–2640)	0.73 ± 0.727 (0.13–2.74)
<i>A. tamaense</i> N = 15 Fig. 8	Pure tone short	22 ± 57 (13–30)	1209 ± 897 (103–3802)	n/a	n/a	2290 ± 48 (2210–2380)	2850 ± 62 (2730–2970)	2590 ± 36 (2540–2640)	0.11 ± 0.033 (0.05–0.19)

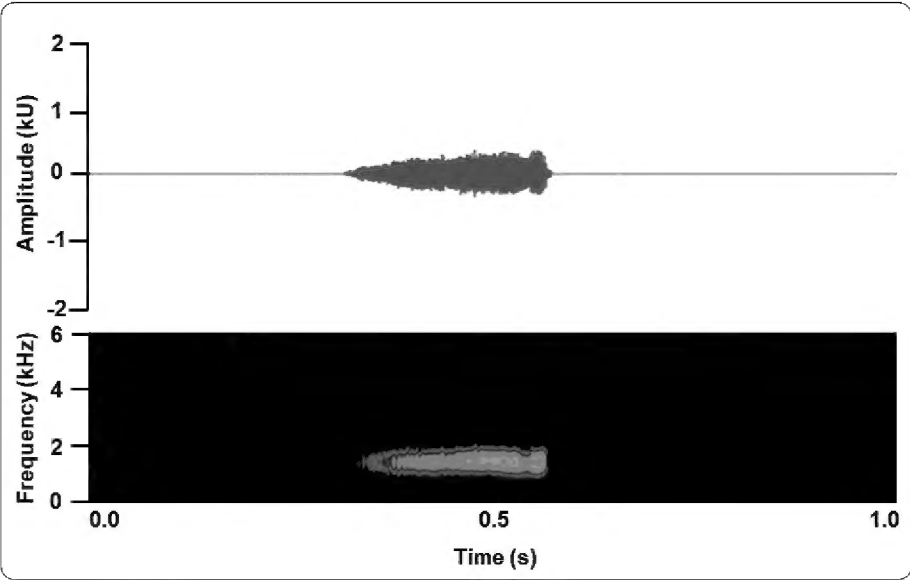


Figure 4. Oscillograms and spectrograms of a pure tone call of *A. carbonerensis* (from series SMNS 11941), recorded 10 June 1987 at Eusebio Forest (2,330 m a.s.l.), La Carbonera, Mérida State; distance to recorder ca. 1.5 m; temperature not taken.

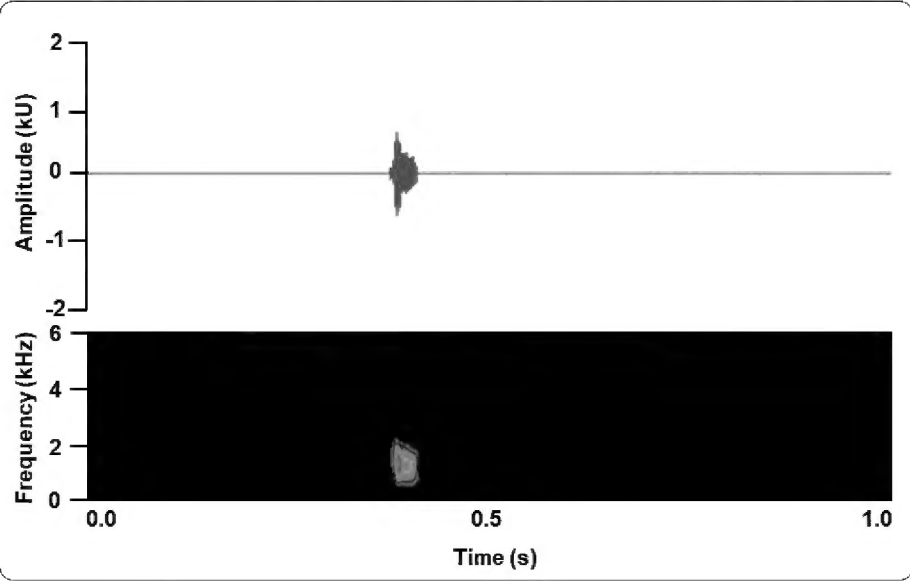


Figure 5. Oscillograms and spectrograms of a pure tone short call of *A. carbonerensis* (from series SMNS 11941), recorded 10 June 1987 at Eusebio Forest (2,330 m a.s.l.), La Carbonera, Mérida State; distance to recorder ca. 1.5 m; temperature not taken.

They are considerably different in duration. In one series (Fig. 4), they resemble the frequency-modulated ‘typical’ pure tone calls described for other *Atelopus* species (Cocroft et al. 1990; Lötters et al. 2002a). The other call (Fig. 5) is markedly shorter than pure tone calls (sensu Cocroft et al. 1990) in any other *Atelopus* species (the shortest known is that of *A. mucubajiensis*, Table 3). Moreover, its frequency is modulated downwards, resembling the unpulsed short call (sensu Cocroft et al. 1990) of *A. varius* (and apparently *A. nahumae*, although its short call is markedly longer than in other congeners; Ortega et al. 2017). Cocroft et al. (1990) concluded that, in *Atelopus* species, short calls are either pulsed or unpulsed, as they recorded the second mentioned only in a population of *A. varius* that they allocated to *A. zeteki*, which, at the same time, did not produce pulsed short calls. However, as both populations are allocable to *A. varius* (cf. Richards and Knowles 2007; R. Ibáñez pers. comm.), this species apparently produces both call types. Likewise, *A. carbonerensis* emits both the typically pulsed (Fig. 3) and an unpulsed short call (Fig. 5), even in specimens from the same population. Therefore, we rather advocate that, in *Atelopus*, two short call types exist: pulsed short calls and pure tone short calls (Tables 1, 3).

It is important to note that both pure tone calls and pure tone short calls were emitted in a series along with pulsed short calls. Little is known about the function of *Atelopus* pure tone calls, as these ‘whistles’ have been observed in a few species only (Table 1). Jaslow (1979) noted them in close-range encounters of *A. chiriquiensis* males, suggesting that they are aggressive calls, sensu Wells (2007). However, Lötters et al. (2002a) stated that in captivity, male *A. reticulatus* produced pure tone calls even when no other males were present.

The function of the pure tone short call remains even less clear, but in *A. nahumae*, it was interpreted as a release call (Ortega et al. 2017). At least for *A. carbonerensis*, we confirm that all three call types are emitted during close-range interactions with physical contact amongst conspecific males and, thus, are in the range of aggressive and release calls. Perhaps these observations are in line with those of Wells (2007), who stated that anuran vocalisation repertoires can be complex.

With four structural call types recognised, *A. carbonerensis* is the member of the genus with the largest call repertoire known (Table 1). Cocroft et al. (1990) mentioned ‘other calls’ which can be interpreted as partial or intermediate calls of the known call types. Our recordings of *A. carbonerensis*, in addition, contain vocalisations that might very well represent either partial or intermediate calls.

Atelopus mucubajiensis

On different occasions, we were able to obtain pure tone and pure tone short calls (as defined above) from this species (Figs 6, 7, Table 3). The first mentioned is similar to pure tone calls in other *Atelopus* species (Cocroft et al. 1990), but it is frequency-unmodulated and shows harmonics. Pure tone calls in *A. mucubajiensis* are shorter than in other members of the genus and thus feature the lowest known range of this structural call type in the genus (so far 180–290 ms in *A. cruciger*, Cocroft et al. 1990), while the upper range is represented by *A. reticulatus* (see above). As in *A. carbonerensis*, pure tone short calls exhibit a descending frequency modulation, but they last slightly longer in *A. mucubajiensis* (Table 3).

The identity of the specimen emitting pure tone calls, however, remains tentative. It was neither seen nor collected. Indeed, no other anurans producing such ‘typical’ *Atelopus* pure tone calls are known from the site. Alternatively, it may be considered that a female *A. mucubajiensis* produces the pure tone calls recorded, as at least in one other member of the genus, females can emit calls while in physical interaction with other specimens (Rocha Usuga et al. 2017).

The pure tone short call was emitted by a male in amplexus with a female in a collection bag; no other conspecifics were present. As afore-mentioned, the function of pure tone short calls is poorly understood but they may play a role in close-range intraspecific communication (see *A. carbonerensis*). However, the absence of conspecifics (other than the amplexant female) further complicates their interpretation in *A. mucubajiensis*.

Atelopus tamaense

When the type series of this species was collected, vocalisations of one male were recorded while handling. It is a pure tone short call and thus *A. tamaense* is the fifth *Atelopus* species (besides the two described above, plus

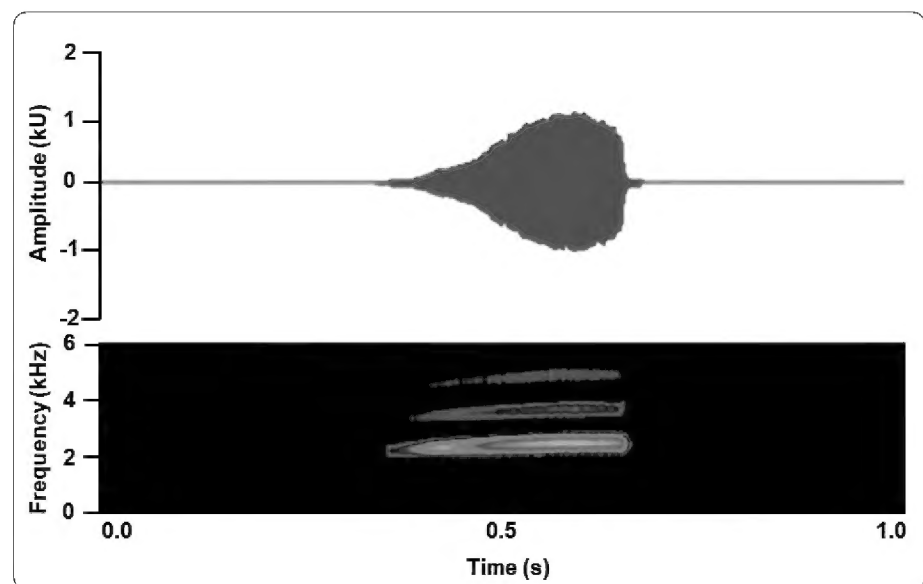


Figure 6. Oscillogram and spectrogram of a pure tone call of *A. mucubajiensis* (specimen not collected), recorded 23 June 1982 at La Corcovada, Páramo de Mucubají (3,050 m a.s.l.), Mérida State; distance to recorder ca. 2 m; 13.5 °C air temperature.

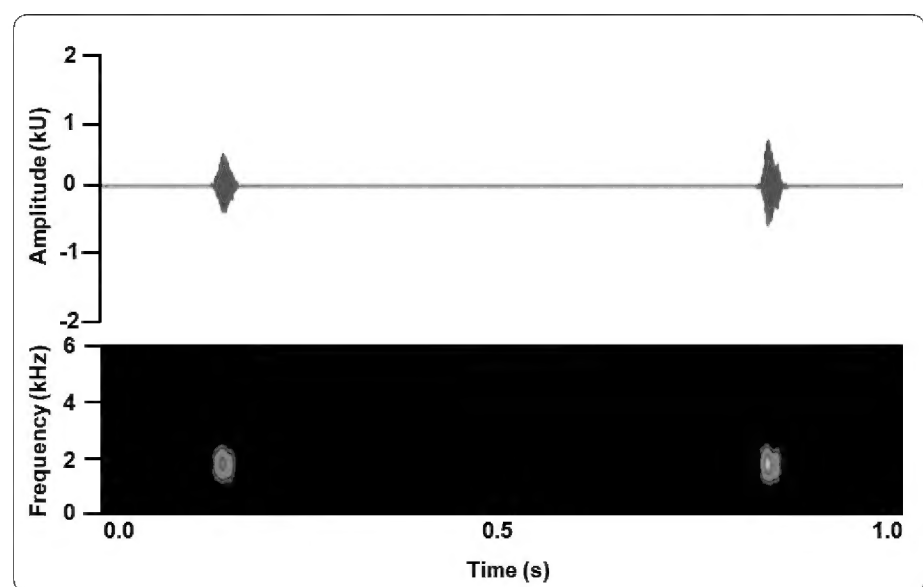


Figure 7. Oscillogram and spectrogram of pure tone short calls of *A. mucubajiensis* (ULABG 2641), recorded 7 June 1989 at La Corcovada, Páramo de Mucubají (3,000 m a.s.l.), Mérida State; distance to recorder ca. 0.3 m; temperature not taken.

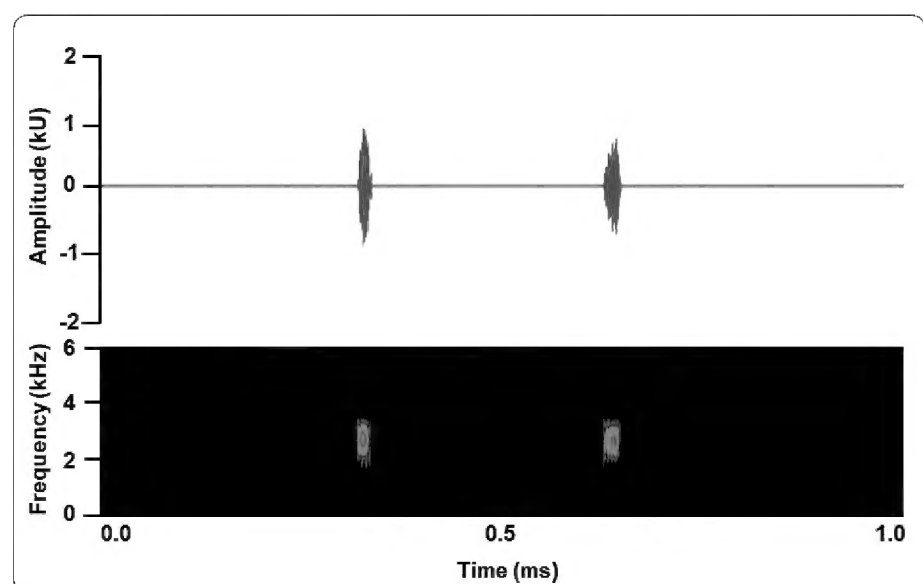


Figure 8. Oscillogram and spectrogram of pure tone short calls of *A. tamaense* (ULABG 1820), recorded 12 August 1987 at Páramo de Tamá (2,950 m a.s.l.), Apure State; distance to recorder < 2 m; temperature not taken.

A. nahumae and *A. varius*) from which this call type is known. It is similar in duration to that of *A. carbonerensis* (Table 3), but it is frequency-modulated (Fig. 8). As already stated, the function of *Atelopus* pure tone short calls

remains enigmatic. They may be emitted during close-range interactions with physical contact of conspecifics (i.e. in the range of aggressive and release calls, see *A. carbonerensis*). Thus, it may be assumed that handling the *A. tamaense* specimen has acted as a trigger to vocalise.

Conclusions

Bioacoustics in the genus *Atelopus* remain poorly understood. One reason is that, including the present paper, vocalisations of only 23 of more than 100 species are known; a fact that is apparently linked to the dramatic declines which these amphibians have undergone. Moreover, the call repertoire is more complex in the genus than previously supposed and behavioural contexts are not entirely clear. We suggest that, instead of three, four call types emitted by males should be distinguished by structure and duration, which show some overlap in duration across the entire genus, but not within species (Table 1): (1) pulsed calls, 92–1240 ms, known in 16 species, interpreted to represent advertisement calls; (2) pure tone calls, 159–420 ms, known in six species, most likely to be aggressive calls; (3) pulsed short calls, 5–171 ms, known in 11 species, clearly representing release calls; (4) pure tone short calls, 8–135 ms, known in five species, with unclear function. The duration of pulsed calls and pulsed short calls shows some overlap across species, but the two call types are unambiguously distinguished for each single species. So far, *A. carbonerensis* is the only member of the genus in which all four structural call types are present. However, we assume that this rather reflects a lack of information and expect that also in other species more call types, if not all of them, exist. This once more underlines that *Atelopus* bioacoustics are a research field of high potential.

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Supplementary material 1

Atelopus carbonerensis various call recorded by DM

Authors: Stefan Lötters, Dietrich Mebs, Gunther Köhler, Joseph Vargas, Enrique La Marca

Data type: WAV file

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Supplementary material 2

Atelopus carbonerensis pulsed call recorded by ELM

Authors: Stefan Lötters, Dietrich Mebs, Gunther Köhler, Joseph Vargas, Enrique La Marca

Data type: WAV file

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Supplementary material 3

Atelopus carbonerensis short call recorded by ELM

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Supplementary material 4

Atelopus mucubajiensis pure tone call recorded by ELM

Authors: Stefan Lötters, Dietrich Mebs, Gunther Köhler, Joseph Vargas, Enrique La Marca

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Supplementary material 5

Atelopus mucubajiensis pure tone short call recorded by ELM

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Supplementary material 6

Atelopus tamaense pure tone short call recorded by ELM

Authors: Stefan Lötters, Dietrich Mebs, Gunther Köhler, Joseph Vargas, Enrique La Marca

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